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ABSTRACT

The deep-sea gorgonian octocoral *Primnoa resedaeformis* is distributed throughout the Atlantic and Pacific Oceans at depths of 65 - 3200 m. It has a two-part skeleton of calcite and gorgonin. Towards the inside of the axial skeleton gorgonin and calcite are deposited in concentric growth rings, similar to tree rings. Colonies were collected from the Northeast Channel (northwest Atlantic Ocean, southwest of Nova Scotia, Canada) from depths of 250 – 475 m. Radiocarbon was measured in individual rings isolated from sections of each colony, after dissolution of calcite. Each $\Delta^{14}C$ measurement was paired with a ring age determined by three amateur ring counters. The precision of ring counts averaged better than ± 2 years. Accurate reconstruction of 20^{th} century bomb-radiocarbon shows that 1) the growth rings are formed annually, 2) the gorgonin is derived from surface particulate organic matter (POM) and 3) useful environmental data are recorded in the organic endoskeletons of deep-sea octocorals. These results support the use of *Primnoa resedaeformis* as a long-term, high resolution monitor of surface ocean conditions, particularly in temperate and boreal environments where proxy data are lacking.

Keywords: *Primnoa*, deep-sea coral, octocoral, growth rings, gorgonin, bomb radiocarbon

Running head: Annual growth rings in a deep-sea octocoral

INTRODUCTION

For generations, fishermen in Atlantic Canada have known about the occurrence of habitat-forming, deep-sea corals offshore (Breeze et al. 1997). There has been recent interest in using these corals as historical monitors of deep and intermediate water mass variability (Smith et al.1997, Frank et al. 2004). This interest stems from the fact that deep-sea corals generally live for hundreds of years or more and their skeletons contain discrete growth layers (Druffel et al. 1995, Risk et al. 2002, Adkins et al. 2004). Geochemical sampling of these layers may provide long-term, high resolution records of proxy climate information, far beyond the range of instrumental records (Heikoop et al. 2002, Roark et al. 2005).

The deep-sea gorgonian coral *Primnoa resedaeformis* is one of the dominant corals found off eastern Canada, particularly in canyons along the shelf break (Breeze et al. 1997). It is also distributed throughout the Atlantic and Pacific Oceans at depths of 65-3200 m (Smithsonian holdings: http://goode.si.edu/webnew/pages/nmnh/iz/Query.php). The arborescent skeletons of *P. resedaeformis* are made up of calcite and gorgonin, a tough horny protein, deposited in concentric rings (Risk et al. 2002). Three growth zones are evident: 1) an inner "central rod" and 2) "horny axis", both made of calcite and gorgonin, and 3) an outer "calcite cortex", containing practically no gorgonin (Sherwood 2002). Growth rings in the horny axis are visible as light-dark couplets; the darker parts contain a higher percentage of gorgonin:calcite (Risk et al. 2002). Rings in the calcite cortex are more ambiguous; often they are barely visible as slight differences in translucence. Using ^{210}Pb dating, Andrews et al. (2002) inferred that the growth rings in

an Alaskan *P. resedaeformis* are formed annually. Based on radiocarbon (Risk et al. 2002) and U/Th dating (Scott et al. in press) of fossil *P. resedaeformis* specimens collected near Georges Bank, life-spans of individual colonies may exceed several hundreds of years.

In this paper, we use bomb-produced radiocarbon to validate annual ring formation in colonies of *P. resedaeformis* collected off Nova Scotia, Canada. Oceanic uptake of bomb-^{14}C produced by atmospheric nuclear weapons testing in the late 1950s and early 1960s provides a time-varying tracer. In the North Atlantic, the timing of the increase is well constrained from direct measurements of dissolved inorganic carbon (DIC; Nydal et al. 1998) and indirectly, from measurements of ^{14}C in annually-banded reef corals from Bermuda and Florida (Druffel 1989), and a long-lived quahog (*Arctica islandica*) from Georges Bank (Weidman & Jones 1993). The initial rise of bomb-^{14}C in the surface ocean provides a unique time-marker which may be used to establish or validate skeletal chronology (Kerr et al. 2005). Additionally, if one knows the year of the post-bomb maximum for a certain location or water-mass the post-bomb peak itself can be used as a reference tie point (e.g. Roark et al. 2005). Since the gorgonin fraction of gorgonian corals is formed from recently exported particulate organic matter (POM; Griffin and Druffel 1989; Roark et al. 2005; Sherwood et al., in review), we expect that living colonies of *P. resedaeformis* incorporated the bomb-^{14}C pulse. We focus on younger colonies (< 75 years), so that rings in the horny axis may be dated more easily.

MATERIALS AND METHODS

Colonies of *Primnoa resedaeformis* were collected offshore Nova Scotia, Canada, from the Northeast Channel (approx. 42°00 N/ 65°50 W), located between Georges and Browns bank, at depths of 250-475 m. Collections were made in August 2001, during an expedition using the remotely operated submersible ROPOS aboard the CCGS Martha Black, and in the summer of 2002, by trawl, during routine oceanographic surveys conducted by the Bedford Institute of Oceanography. Some of the specimens were frozen at the time of collection, others were air-dried. Skeletal sections were cut from the thickest part of each recovered colony using a rock saw. The sections were ground and polished on a diamond lap wheel and photographed with a digital camera in macro mode under UV light. The UV light improves the appearance of ring couplets and makes it easier to distinguish the rings from cracks in the sections (Fig. 1).

To isolate the gorgonin fraction for radiocarbon assays, the sections were dissolved in 5% HCl until reaction ceased, which took up to 3 weeks. The sections were then placed in a Petrie dish filled with distilled water and the rings were picked apart with tweezers and scalpel under a binocular microscope, starting at the outside of each section, and moving in toward the centre. The exact position of each sample on a section was marked on photographic prints overlain with transparency film. The separated rings were placed in 5 ml polyethylene vials, topped with 5 % HCl and left for an additional 2 days to ensure that all of the calcite dissolved. Afterwards, samples were triple-rinsed in de-ionized water and dried at 70 °C overnight. From each colony, anywhere from 1 to 10 rings were selected for ^{14}C analysis, depending on colony age and the ease with which the

annual ring couplets could be identified and counted. Samples were preferentially selected to bridge the expected rise in bomb-^{14}C between 1958 and the early 1970s, because this provides the best constraint on chronology. Samples were combusted in individual quartz tubes and reduced to graphite in the presence of iron catalyst. Delta-^{14}C was determined on graphite targets at the Center for AMS. Results include a background and $\delta^{13}C$ correction and are reported as $\Delta^{14}C$ according to Stuiver and Polach (1977).

To obtain ring counts as objectively as possible, the photographic prints of each section were circulated randomly among departmental colleagues with no prior experience in counting rings in gorgonian corals or any other organism. The prints were overlain with a second layer of transparency film, with the first transparency flipped off. Ring counters were briefed for 5 minutes on how to identify an annual ring. They were then asked to mark the positions of annual rings on the second transparency. This involved drawing a line radially across parts of the sections where rings could be seen the easiest, and marking the annual rings along that line (Fig. 1). Each ring identified was assigned to a calendar year based on whether the outermost layer represented 2001 or 2002, depending on the year of collection. In 2 of the 7 colonies, there was tissue necrosis on the outer margin of the skeleton. For these "dead" colonies, a chronological control point was provided by the peak in $\Delta^{14}C$ (see below). Afterwards, the first transparency was replaced, and calendar years were paired with the rings isolated earlier. The counting experiment was repeated three times by different counters.

RESULTS

The precision of growth ring counts, as measured by the standard error among three different ring counters, averaged ± 1.2 years (Table 1). Ages ranged from 24 - 78 years. The standard error increased slightly with age, as expected, because the chronological error is compounded with increasing age. The spread in values reflected differences in the "quality" of rings viewed in different sections. The least precise age estimates were generated on the older sections; but these were still relatively good (± 3.5 years).

The accuracy of growth ring counts is demonstrated in a plot of $\Delta^{14}C$ against calendar year (Fig. 2). Data from the 5 live colonies clearly indicated that the peak in $\Delta^{14}C$ occurred around 1972. Additional data from the two “dead” colonies were added to the figure by using 1972 as a chronological control point. An all-time high of +90 ‰ was measured in one colony, so this point was assigned to the year 1972. In the other specimen, a spline curve was fit through a plot of $\Delta^{14}C$ versus ring number in order to determine which ring number should be assigned to 1972.

The $\Delta^{14}C$ curve for *P. resedaeformis* is identical to that previously measured in an ocean qhahog (*Arctica islandica*) collected at a depth of 75 m on nearby Georges Bank (Weidman & Jones 1993; Fig. 2). A similar curve based on the otoliths of haddock (*Melanogrammus aeglefinus*) collected on the southern Grand Banks has also been published (Campana 1997; Fig. 2). The *P. resedaeformis*, *A. islandica*, and *M. aeglefinus*

curves all range from a pre-1958 low of ~ -80 ‰ to an early 1970s peak of ~ +80 ‰, followed by a gradual decrease to ~ +40 ‰ to the present.

DISCUSSION

The growth ring counting method used here is a relatively simple and effective way to age specimens of *P. resedaeformis* with an acceptable level of precision (SE < 2 years). The counters had no previous training in growth ring counting and were not asked to count any more than 3 specimens each, so no one individual became an expert counter. The precision of ring counts largely depended on the quality of the sections. In some cases the growth rings were very narrow, making counting difficult. Sub-annual rings (Risk et al. 2002) could have been mistaken for annual rings. In addition, "calcite cortex" material was sometimes inter-layered with the horny material. Gorgonians colonies may bend and twist throughout their lives to keep their fans oriented perpendicularly to prevailing currents (Wainwright & Dillon 1969). These growth variations affect the appearance of rings. Therefore, future studies involving ageing of *Primnoa* should select for the straightest and highest quality colonies. Similar considerations are routine in dendochronology and sclerochronology.

Samples for $\Delta^{14}C$ and growth ring counts were made on the same sections, such that each $\Delta^{14}C$ measurement had a matching calendar age. Data from eight different colonies were used to establish a twentieth century record of $\Delta^{14}C$. This record was identical to previously published $\Delta^{14}C$ records derived from a mollusc shell (Weidman & Jones 1993) and haddock otoliths (Campana 1997) collected from the NW Atlantic. The

P. resedaeformis $\Delta^{14}C$ curve is also in phase with the record from annually banded reef coral skeletons from Florida and Bermuda (Druffel 1989), and with direct measurements of surface water DIC (Nydal et al. 1998). The results are consistent with the interpretation that the ring couplets found in the horny axis region of *P. resedaeformis* are formed annually.

Andrews et al. (2002) also validated annual ring formation in an Alaskan *Primnoa*; however, they measured the rate of decay of ^{210}Pb over the length of a colony to validate growth ring counts. Among shallow water gorgonians, annual growth rings have also been demonstrated by non-radiometric methods. Usually, this has involved the correspondence in age estimated from the height of a colony with the age estimated from growth rings (e.g. Grigg 1974). The method described here is a more direct way of validating annual growth rings, since $\Delta^{14}C$ and age determinations were made on the same sections.

Similarity in the range and timing of $\Delta^{14}C$ measured in *P. resedaeformis* growing between 250-475 m with *A. islandica* growing at 75 m on Georges Bank suggests that the skeletons of these organisms are derived from the same pool of DIC. The carbonate shell of *A. islandica* incorporates ^{14}C directly from DIC (Weidman & Jones 1993). The shelf waters on Georges Bank are well mixed; so DIC will have about the same $\Delta^{14}C$ from 0 - 75 m. In contrast to Georges Bank, the slope waters which occupy the Northeast Channel are stratified. If the gorgonin in *P. resedaeformis* were derived from ambient DIC at depth, $\Delta^{14}C$ would be much lower than actually measured (Bauer et al. 2002). As in

shallow-water gorgonians that have been studied in situ (e.g. Ribes et al. 1999), zooplankton and sinking POM probably constitute the main diet of this species. Therefore, ^{14}C is assimilated by phytoplankton in surface waters, and is incorporated by *P. resedaeformis* via the plankton food web. The lack of a time lag in peak $\Delta^{14}C$ rules out the possibility that *P. resedaeformis* feeds on older, more refractory POM, as we have found with $\delta^{15}N$ data (Sherwood et al., in review). These results corroborate earlier work showing that gorgonin is derived from sinking POM (Griffin & Druffel 1989, Roark et al. 2005).

The range of $\Delta^{14}C$ values measured in *P. resedaeformis*, *A. islandica*, and *M. aeglefinus* (~ -80 to ~ +80 ‰) is depleted compared to reef coral records from Florida and Bermuda (~ -60 to ~ +160 ‰; Druffel 1989). This difference has been explained by the supply of $\Delta^{14}C$-depleted Labrador Sea water to the NW Atlantic shelf and slope (Weidman & Jones 1993). In the subtropics, more intense stratification prevents dilution of the bomb signal by $\Delta^{14}C$-depleted deep waters.

From a paleoceanographic standpoint, the formation of annual rings makes *P. resedaeformis* analogous to reef scleractinian corals. Geochemical proxy records from reef corals have been a mainstay of Holocene paleoceanography ever since Knutsen et al. (1972) conclusively demonstrated annual timing of density bands with ^{90}Sr. Accurate reconstruction of 20th century surface water $\Delta^{14}C$ demonstrates that useful environmental data are recorded in the organic fraction of *Primnoa* skeletons. In addition, the stable C and N isotopic composition of gorgonin may reflect surface water productivity (O. A.

Sherwood et al. unpubl.); thus, long term, high resolution reconstructions of surface processes may be feasible (Heikoop et al. 2002). The oldest colony in the present study was 78 years; but, colonies may live for at least 320 years (Risk et al. 2002). Useful information on ambient conditions at depth may also be contained in the skeletal calcite, since this fraction is derived from ambient DIC at depth (Griffin and Druffel 1989, Roark et al. 2005).

There has been increasing interest in the frequency of climate forcing mechanisms such as the North Atlantic Oscillation. High-resolution proxy reconstructions from *Primnoa* may help to resolve the "spectral gap" issue between instrumental and proxy-based climate records, particularly in temperate and boreal environments, where proxy marine climate data are lacking.

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Table 1. Summary of *P. resedaeformis* sections used in growth ring counting and $\Delta^{14}C$ determinations. Average year and standard error calculated from 3 different ring counters.

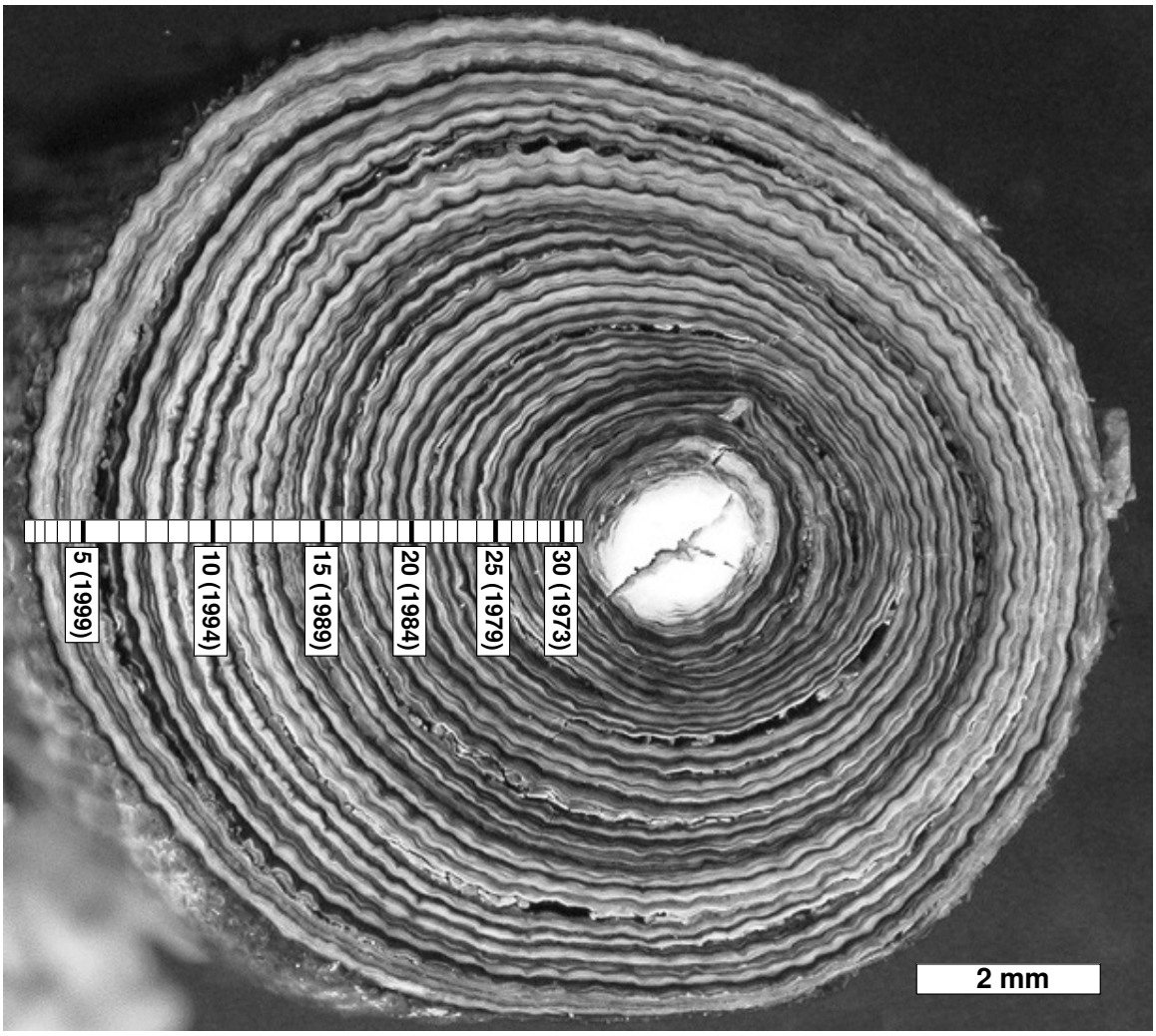
Section	Ring no.	Avg. year	SE	CAMS # [a]	$\Delta^{14}C$ (‰)	±
DFO-2002-con5A1	5	1990	1.9	97097	36	5
DFO-2002-con5A1	10	1979	2.4	97098	52	4
DFO-2002-con5A1	16	1970	2.8	97099	71	4
DFO-2002-con5A1	21	1965	2.4	97100	59	4
DFO-2002-con5A1	25	1960	2.1	97101	-47	3
DFO-2002-con5A1	31	1953	2.1	97102	-77	3
DFO-2002-con5A1	37	1948	2.2	97103	-80	3
DFO-2002-con5A1	43	1942	2.8	97104	-72	3
DFO-2002-con5A1	50	1934	3.3	97105	-77	3
DFO-2002-con5A1	58	1924	3.3	97106	-72	3
HUD-2002-055-VG15-A3	10	1981	0.6	111140	67	4
HUD-2002-055-VG15-A3	19	1971	0.7	111142	90	4
HUD-2002-055-VG15-A3	27	1963	1.7	111143	-18	5
HUD-2002-055-VG13-2	22	1980	1.5	111139	59	4
NED-2002-037.46-1A	1	2002	0.3	111328	33	5
NED-2002-037.46-1A	16	1984	0.6	111329	68	5
NED-2002-037.46-1A	58	1947	0.7	111330	-82	4
NED-2002-037.46-5-1	25	1978	1.2	111331	63	4
ROPOS-639009-C4	19	1972	0.9	111623	82	4
ROPOS-639009-C4	27	1963	1.5	111624	-46	4
ROPOS-639009-C4	40	1951	0.3	111625	-70	3
ROPOS-6400013-E1	10	1994	1.2	111626	52	4
ROPOS-6400013-E1	15	1989	1.5	111141	54	4
ROPOS-6400013-E1	20	1984	1.5	111627	67	5
ROPOS-6400013-E1	25	1979	1.9	111628	61	4
ROPOS-6400013-E1	31	1972	3.3	111629	82	4

[a] Centre for Accelerator Mass Spectrometry analytical identifier

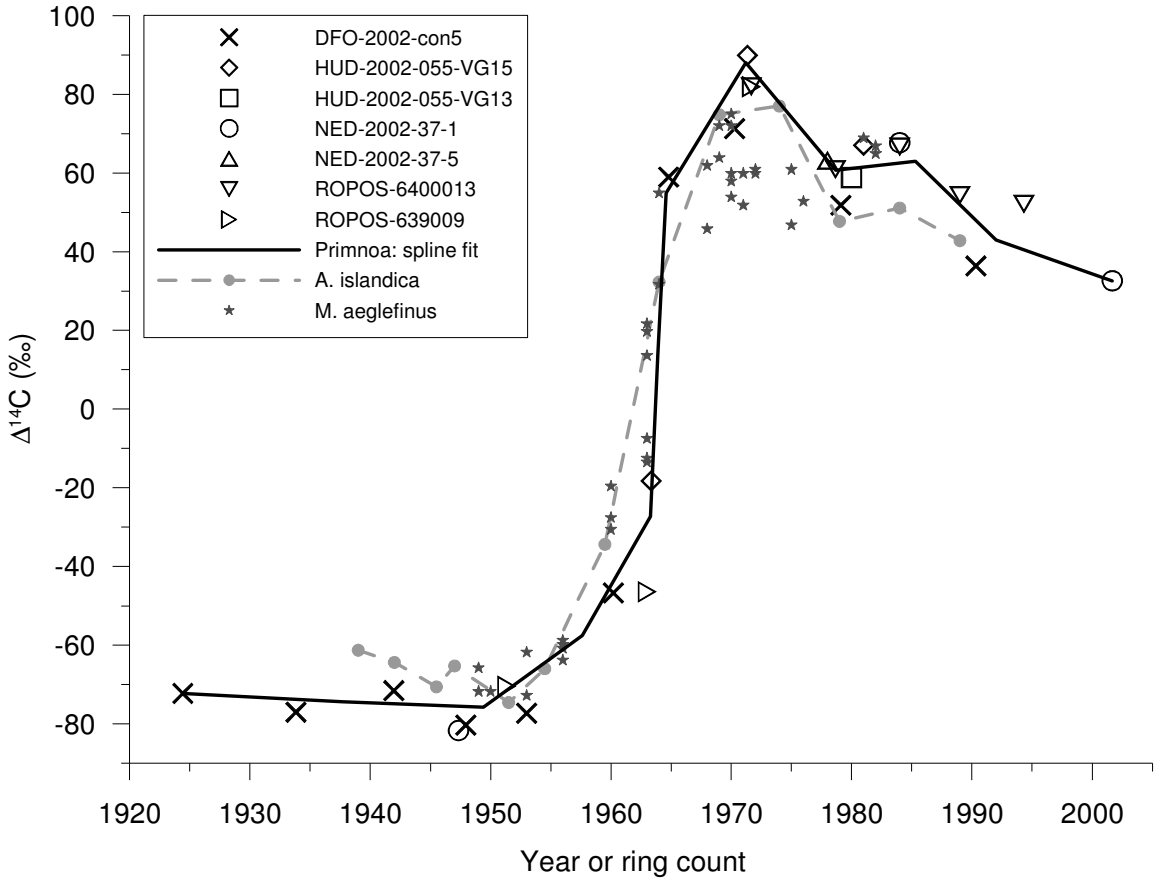
FIGURE CAPTIONS

Fig. 1. Example section of *Primnoa resedaeformis* (colony ROPOS-6400013; collected live in 2001). Lighter centre is the central rod; outer banded section is the horny axis. Calcite cortex is not present. Markings show individual rings isolated in preparation, with corresponding calendar age (in brackets), as determined by 3 amateur counters.

Fig. 2. Plot of $\Delta^{14}C$ vs age for 7 different colonies of *P. resedaeformis* collected in the NE Channel. A spline fit is drawn through the data. Also shown are the data from *A. islandica,* collected at a depth of 75 m on nearby Georges Bank (Weidman & Jones 1993) and haddock otoliths collected on the Grand Banks (Campana 1997).



Sherwood et al., Fig. 1



Sherwood et al., Fig. 2